BOTANICAL GAZETTE

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Leaf movement in Cercis Canadensis.

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WITH PLATES XIX AND XX.

Among the numerous observations which have been made concerning leaf movement the bulk of attention has probably been given to the investigation of the especially interesting phenomena connected with Mimosa pudica. The histological structure and development of the unusually sensitive pulvinus of this plant has been quite fully described. Numerous other members of the Leguminosæ have well marked pulvini and offer admirable opportunities for physiological and histological study. *Cercis Canadensis* L., while presenting less noticeable leaf movement than the sensitive plant, proves on closer examination to be a very interesting subject for investigation.

In external appearance the pulvini on a mature leaf of Cercis Canadensis consist of prominent enlargements at both the upper and lower end of the petiole. The enlargement at the junction of the petiole and leaf lamina is the principal one in producing the leaf movement, while the enlargement at the basal end of the petiole so far as movement is concerned seems to be almost functionless. In a series of observations made on a number of leaves (given in tabulated form later) no movement of any importance could be detected in the basal pulvinus. The upper or true pulvinus of one of the largest leaves found on a thriftily growing tree gave the following measurements.

Length on upper surface	5. mm
Length on lower surface	7.5 mm
Horizontal diameter, lower end	3. mm
Horizontal diameter, upper end	2.5 mm
Average horizontal diameter of petiole	2. mm
Average vertical diameter of petiole	1.8 mm

In the true or upper pulvinus, which shall receive the bulk of attention in this paper, the upper end may be said to form a portion of the upper surface of the lamina of the leaf, while the leaf veins, seven in number, of which the central one is probably twice the size of either of the others, are given off from its margin. An upper view of the mature pulvinus is given in plate XX, fig. 3. When a mature pulvinus presents a series of transverse markings or wrinkles it may be taken as an indication that the leaf is capable of very great movement. This is found to be quite true in the case of the plant under study. In a series of observations made on a number of leaves at different times during the day it was found that the angle between the petiole and the lamina varied nearly 100 degrees. With slight modifications due to variations in temperature and light the daily movement of the leaf may be said to be as follows: The rise, beginning approximately at 3 A. M. is continued quite rapidly until 9 A. M. A slight decline then occurs, the lamina again rising to near its forenoon position at about 2 P. M. After this time rapid falling takes place, the full sleep position being reached at about 10 P. M.

1. MOVEMENT OF UPPER PULVINUS. FIRST DAY.

TIME OF DAY.	ANGLE OF LEAF-BLADE WITH PETIOLE IN DEGREES.						TEMPERATURE. °F.	AVERAGE MOVEMENT IN DEGREES.
	LEAF 1.	LEAF 2.	LEAF 3.	LEAF 4.	LEAF 5.	LEAF 6.		
2:30 A.M.	41	41	21	30	32	18	80	52.16
5	93	97	63	90	75	78	82	16.33
6	104	113	78	102	97	100	82	13.33
7	118	127	88	117	111	113	76	– 3.16
8	112	127	82	118	105	111	76	– 8.
9	92	129	78	104	97	107	76	– 3.66
10	91	125	79	90	96	104	85	–12.83
11	85	118	67	75	72	91	87	– 8.83
12 M.	83	112	56	60	67	77	88	1.5
1 P. M.	88	104	60	61	68	83	88	6.66
2	95	111	63	73	71	91	85	9.16
3	105	125	73	81	84	91	80	6.33
4	114	128	80	91	90	94	78	17.83
5	127	144	92	113	116	112	76	– 9.16
6	112	131	95	113	103	95	71	–14.33
7	101	114	85	87	90	86	71	–16.83
8	84	91	74	70	71	72	67	–15.16
9	71	77	58	58	57	50	65	–10.83
10	60	61	43	60	46	36	66	

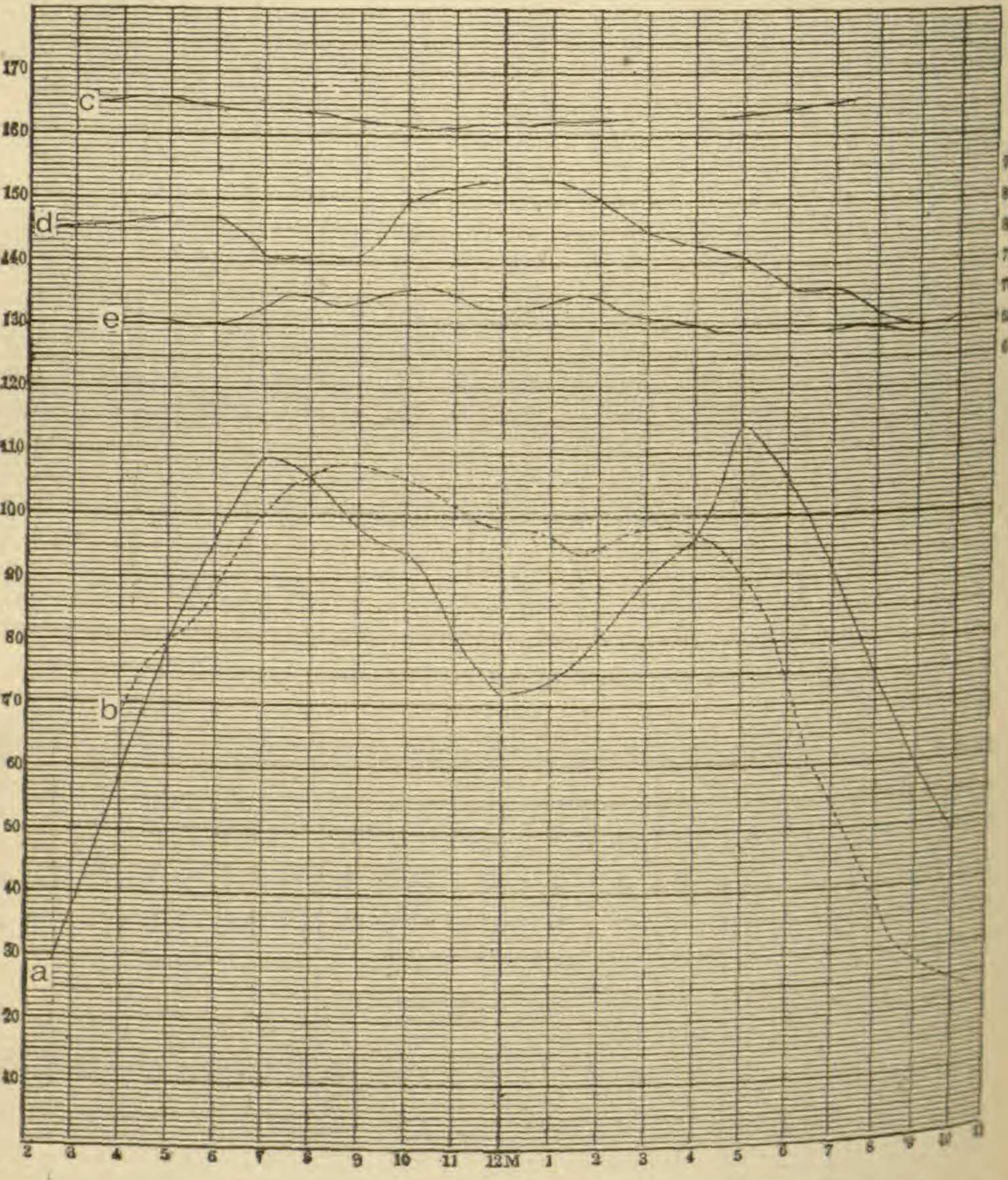
2. MOVEMENT OF UPPER PULVINUS. SECOND DAY.

TIME OF DAY.	ANGLE OF LEAF-BLADE WITH PETIOLE IN DEGREES.						TEMPERATURE. °F.	AVERAGE MOVEMENT IN DEGREES.
	LEAF 1.	LEAF 2.	LEAF 3.	LEAF 4.	LEAF 5.	LEAF 6.		
4 A.M.	85	81	51	76	71	65	66	
4:30	91	91	59	81	81	76	66	8.33
5:30	97	101	68	85	82	89	65	7.16
6:30	105	114	80	100	94	101	66	12.
7:30	119	124	89	106	100	110	70	9.
8:30	121	131	90	115	104	113	68	4.33
9:30	127	131	90	113	101	106	70	— 1.
10:30	123	134	91	96	90	116	71	— 3.
11:30	115	125	90	93	87	111	68	— 4.83
12:30 P.M.	110	122	92	92	88	113	68	— .66
1:30	108	118	85	89	84	109	70	— 4.
2:30	110	123	90	90	84	114	67	3.
3:30	115	120	94	90	83	112	66	.5
4:30	116	120	94	83	75	110	64	— 2.66
5:30	109	109	95	69	59	97	64	—10.
6:30	85	80	71	51	40	65	64	—24.33
7:30	72	68	55	38	24	46	65	—14.83
8:30	56	51	37	24	19	29	64	—14.5
9:30	49	40	29	23	17	30	64	— 4.66
10:30	45	37	21	20	17	30	64	— 3.

3. MOVEMENT OF LOWER PULVINUS.

TIME OF DAY.	ANGLE OF PETIOLE WITH STEM IN DEGREES.												TEMPERATURE °F.	AVERAGE MOVEMENT IN DEGREES.
	LEAF 1.	LEAF 2.	LEAF 3.	LEAF 4.	LEAF 5.	LEAF 6.	LEAF 7.	LEAF 8.	LEAF 9.	LEAF 10.	LEAF 11.	LEAF 12.		
3:30 A.M	180	146	150	180	172	160	165	150	143			171	66	
4:30	180	148	152	180	174	162			143	171	175	171	66	.8
5:30	178	150	152	180	175	160	169	150	146	165	173	171	65	– .6
6:30	175	146	150	180	172	163	168	151	144	167	172	166	66	–1.25
7:30	177	146	152	177	172	163	171	150	144	163	172	169	70	.16
8:30	171	142	150	176	171	160	168	150	145	167	173	170	63	–1.08
9:30	170	143	151	174	170	160	166	149	143	163	168	170	70	–1.33
10:30	170	143	150	176	169	158	165	148	140	163	166	168	71	– .92
11:30	171	143	151	174	171	158	168	149	144	162	163	170	68	.66
12:30 P.M	172	142	150	173	169	161	166	149	142	164	164	168	63	– .33
3:30	170	140	152	176	169	164	168	153	142	164	169	170	66	1.41
4:30	172	141	151	173	165	162	166	154	144	167	169	169	64	– .33
5:30	171	143	152	177	166	162	169	159	142	167	168	168	64	.92
6:30	173	145	150	177	170	164	167	155	146	169	169	169	64	.83
7:30	178	147	154	175	171	162	167	153	145	170	170	169	65	.58

Above in tables 1, 2 and 3, are given the various observations as made on a number of leaves. Tables 1 and 2 show the observations made on the upper pulvinus during two consecutive days. Table 3 shows the observations made on the lower pulvinus during a single day. The time of day at which each observation was made is given in the left hand



LEAF MOVEMENT AND TEMPERATURE CURVES.

column. In the central part of the table are given the exact readings in degrees as made on the separate leaves. In the column at the extreme right is given the average movement in degrees for the entire number of leaves observed, during the time between observations. The downward movement in each case is marked with a negative sign. The temperature at the time the observation was made is given in a column near the right.

These observations were made about the first of March on small plants grown in the green house that were brought from the forest in the previous autumn. The average movement given in the last column in each table together with the temperatures are shown above plotted in the form of curves. Curves *a*, *b*, and *c* correspond respectively with tables 1, 2, and 3. Curves *d* and *e* are temperature curves; *d* corresponding with table 1, and *e* with tables 2 and 3 (the observations in tables 2 and 3 being made at the same time). In plotting curves *a*, *b*, and *c* the average position of the leaves at 5 o'clock A. M. is taken as a starting point in each case, thereby admitting of the graphical representation of the actual position of the leaves at any given time as well as of their average movement. The degrees of the angles are represented on the ordinates, and the time in hours on the abscissæ. The noon point is marked 12 M. Fractions of a degree less than five-tenths are not taken into account, but when five-tenths and over they are counted as one. The degrees of temperature for curves *d* and *e* are indicated at the right near the top. In comparing curves *a* and *b* it will be seen that in *b* the forenoon maximum is reached much later, and that the fall of the leaf in the afternoon takes place much earlier than in *a*. This may be attributed to the fact that in *b* the temperature was much lower than in *a* (see temperature curves *e* and *d* respectively), and that the movements represented by curve *b* were on a cloudy as compared with a bright sunny day in the case of *a*. Curve *c* is to represent the results of the observations made on the basal pulvinus, as given in table 3. The curve seems to indicate a slight decline of the petiole during the middle of the day, but on account of the difficulty experienced in reading the leaf angles to fractions of a degree, I do not feel safe in giving this as a final conclusion. Fig. 1 and 2, plate XIX, are from photographs and show respectively the position of the leaves at night (three o'clock A. M.), as compared with their position in the daytime (eight o'clock A. M).

For the histological investigation of this subject a series of twelve collections were made, beginning with the first swelling of the leaf buds in spring and ending with the mature leaf. The time required for the full development of the leaf is one and a half to two months, or from the first of May to the middle or latter part of June. A goodly amount of each collection was dehydrated in Schultze's dehydrating apparatus and then put in absolute alcohol. In connection with the material as above described a large part of each collection intended for coarser work was placed directly in alcohol. In addition to the supply of alcoholic material a number of young thrifty sprouts were taken from the woods in September and placed in pots in the green-house with the hope of at least inducing an early development of leaves for histological and dynamical study. This experiment was quite successful and leaves both on the old branches and on new shoots sent up from the roots afforded ample supply of material throughout the latter part of winter and early spring for all necessary purposes. The young sprouts developed from the roots were the ones on which the observations on leaf movement as above described were made. The observations were not made, however, until after the leaves had attained almost if not entirely their full development. I also undertook to secure growing material from seeds, but on account of defects in the seed obtained the experiment was unsuccessful.

In the imbedding work, the paraffin method as described by Moll[1] of Groningen, Holland, was used. It was, however, found necessary to modify the method in some respects in order to obtain the best results. The most perfect infiltrations were obtained by subjecting the tissues while in pure turpentine to a temperature of from 40–45° C. for several hours. In all cases the fresh material taken from the greenhouse supply and hardened in picric or chromic acid gave the best results. Very little staining was done, but where undertaken haematoxylin was found to be the most satisfactory.

The mature pulvinus is composed of parenchyma, collenchyma, bast and woody tissue. The parenchyma is probably of first importance, since by changes in its turgescence the movements of the leaf are produced. The collenchyma, which in the petiole comprises the layer of cells immediately under the epidermis, is poorly if at all developed in the pul-

[1] The application of the paraffin imbedding method in botany. Botanical Gazette **13**: 5. 1888.

vinus. The bast which occupies the outer portion of the fibrovascular region forms a complete ring of closely set thick walled cells, and together with the woody tissues evidently constitutes the fulcrum or negative element in producing the leaf movement. By the use of the phloroglucin [2] test for lignin it was found that in the petiole the wood-cells, scalariform vessels and bast were highly lignified, while in the pulvinus only the scalariform vessels with some traces in the wood-cells gave the lignin reaction. The bast in the pulvinus was entirely unlignified and seemed to be much more easily macerated by the acid used in the test than in other parts. In the pulvinus the bast is much more closely packed around the woody tissue, the sieve-tubes and phloem parenchyma being less prominent than in the petiole. The position of these various tissues will be seen by an examination of figs. 4–12 inclusive, plate XX, which are intended, however, to show chiefly the changes in position of the fibrovascular bundles as they pass through the pulvinus. Fig. 4 is from a transverse section made at about the middle point of the petiole. The fibrovascular [3] portions occupy a single completed ring surrounding a centrally placed mass of parenchyma. In fig. 5, which is from a transverse section immediately below the upper pulvinus, the fibrovascular part is divided into two complete rings, in the larger of which there is evidence of still farther subdivision. Figs. 6–11 inclusive are from transverse sections through the upper pulvinus about equally distant from each other from the base to the top. In fig. 6, which is from the lowest section in the series, there is still more evidence of subdivision than in fig. 5; the peripheral parenchyma is more prominent, and the bast is seen to be slightly closer to the woody portions. In figs. 7–11 inclusive the peripheral parenchyma is the prominent feature. The greater diameter of the parenchyma cells seems to be at right angles to the longer axis of the petiole. In fig. 7 the fibrovascular portion is indefinitely and irregularly divided, while in figs. 8, 9 and 10 there seems to be a rearrangement of parts culminating in fig. 10 in three distinct bundles arranged as nearly as possible in a single plane, with the bast tissues closely packed around the woody portions. This is evidently the point of greatest flexure in the

[2] Goodale's Physiological Botany, 14.
[3] See explanation of plates, for lettering of drawings.

pulvinus. Fig. 11 shows the divisions of the fibrovascular parts as they enter the lamina of the leaf. At point *v* is shown a portion of a longitudinal section of one of the veins of the lamina. Fig. 12 is from a dorsiventral median longitudinal section of the upper pulvinus, point *x* being the lower and point *y* the upper end. In this section the fibrovascular portions appear only in a single line as they pass through the pulvinus.

From an examination of the nine drawings just explained it is evident that the fibrovascular bundles, which in the petiole are arranged in a single completed ring, are rearranged as they enter the pulvinus in a plane corresponding with that of the lamina of the leaf, thus offering the least resistance to vertical movement.

Francis Darwin[4] describes the first appearance of the pulvinus in the cotyledons of seedlings of Oxalis corniculata as a transverse zone of longitudinally compressed parenchyma cells. This transverse zone of cells he says makes its appearance about the second day of germination. In the plant under study it is possible to demonstrate leaves in the unopened winter buds of much less development than in the case cited by Darwin. By means of serial longitudinal sections of leaf buds passing dorsiventrally through the leaf petioles, leaves were found in which no evident trace of a pulvinus could be made out. This is true, however, only of the most minute traces of leaves; that is, leaves in which no differentiation into lamina and petiole could be made. In these embryonic leaves the first appearance of the pulvinus may be demonstrated. The pulvinus, as I believe, comprises in the broadest sense simply a continuation of the mesophyll tissue of the lamina down the petiole of the leaf. More carefully stated, it is an enlargement of parenchyma tissue at the upper end of the petiole corresponding both in development and structure with the loose parenchyma of the lamina of the leaf. It is a well known fact that all gradations of connection between the stipules[5] and the lamina of the leaf in various plants can be traced. The stipules may be a part of the lamina, or they may be only partially separated from it leaving a winged petiole, or the petiole may be naked as in the case of Cercis Canadensis leaving the

[4]The Power of Movement in Plants 119. 1881.
[5]Gray's Botanical Text Book, sixth edition, 1: 105–107.

stipules entirely distinct. With equal propriety a portion of the leaf lamina may remain in connection with the petiole and by special modification be changed into an organ for the production of motion. By means of dorsiventral longitudinal sections of the smallest leaves in which a distinction of parts could be made, the structure of the leaf, with the exception of a layer of epidermal cells along the dorsal (lower side when the leaf is expanded) surface together with a few parenchyma cells, was found to be uniform throughout. The next stage of development examined showed traces of scalariform vessels with evident parenchyma in both petiole and lamina. In the largest leaf which could be obtained from an unopened leaf-bud the parenchyma and fibrovascular portions of the petiole and lamina were found to be well developed and at a point in the petiole near the base of the lamina were to be seen a number of parenchyma cells showing evident irregular cell division. This irregular cell division I consider as the first appearance of the pulvinus. It corresponds closely with that taking place in the increasing mesophyll tissue of the lamina of the leaf and is in fact connected with it. Examination of more advanced leaves shows only an increase in number of these irregular cells until the mature pulvinus is reached which is composed in the main of loose irregular parenchyma. In contrasting the first appearance of the motile organ in the plant under study with that noted by Darwin in the case of Oxalis corniculata, I should say that while he observes the first appearance of the zone of cells which is to become the pulvinus from the fact of the transverse regularity of the cells, the exact opposite is true in the case of Cercis Canadensis, the first appearance of the pulvinus becoming evident from the fact of the irregularity of the cell division as contrasted with the regular cell division in the remaining portion of the petiole.

In summary it may be said that the pulvinus of Cercis Canadensis consists in the mature form of collenchyma, parenchyma, bast and woody tissue so arranged as to produce with the least expenditure of energy on the part of the plant under the influence of light a daily movement in the leaf lamina of nearly one hundred degrees. This motile organ is to be considered as a development through multiplication by irregular cell division of a portion of the parenchyma tissue at the upper end of the petiole, and moreover the development of these irregular cells is seemingly in nowise essentially different either in time or character from that taking place in the mesophyll tissue of the lamina of the leaf.

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EXPLANATION OF PLATES XIX AND XX.

Plate XIX.—Cercis Canadensis as affected by light.—Fig. 1. Position of leaves at 3 o'clock A. M.—Fig. 2. Position of leaves at 8 o'clock A. M.

Plate XX.—External and sectional views of petiole and pulvinus of mature leaf.—Fig. 3, × 1⅓; Figs. 4–11, × 30; Fig. 12, × 12. *a*, epidermis; *b*, collenchyma; *c*, peripheral parenchyma; *d*, bast; *e*, sieve tubes and phloem parenchyma; *f*, scalariform vessels and wood cells; *g*, pith parenchyma; *v*, portion of long. section of vein of leaf lamina; *x*, lower end of pulvinus; *y*, upper end of pulvinus. All drawings of sections were made with camera lucida.—Fig. 3. Upper surface of mature pulvinus.—Fig. 4. Trans. section at middle point of petiole.—Fig. 5. Trans. section of petiole immediately below the base of the pulvinus.—Figs. 6–11. Trans. sections approximately 1^{mm} apart, from lower to upper end of upper pulvinus.—Fig. 12. Median dorsiventral long. section of mature upper pulvinus.